

FACTORS AFFECTING ROOT PRODUCTION IN SUBALPINE FORESTS
OF THE NORTHWESTERN UNITED STATES

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ABSTRACT

Root production in subalpine forest ecosystems in the maritime climatic zone of Oregon and Washington is large relative to lowland forests of the region. Moreover, the proportion of ecosystem productivity invested in fine roots and mycorrhizae increases with increasing stand age to a point where over 65% of ecosystem dry matter production occurs in the soil. These subalpine ecosystems occupy habitats having strongly seasonal but abundant precipitation, low evaporative demand, persistent snowpack, a short (130 day) growing season and low soil temperatures.

The principal factor responsible for the large investment in fine roots and mycorrhizae appears to be the availability of mineral nutrients. The primary species in these forests (Abies amabilis, Abies procera, and Tsuga mertensiana) all have larger root systems than required to meet their summer water uptake needs. The species all are well adapted to water uptake in cold soils. Soil gas composition does not appear to play a role in root growth; the major species are quite insensitive to large differences in soil atmosphere O_2 and CO_2 , at least insofar as above- and belowground growth are concerned.

Decomposition and nutrient mineralization processes are slow in this environment so large detritus accumulations are the rule. The dominant (almost exclusive) form of N in these ecosystems is NH_4 , which with PO_4 and SO_4 are nutrient elements that move only very limited distances along concentration gradients toward roots. In such an environment, thorough and repeated exploration of the rooting zone may be the only way trees can obtain nutrients in sufficient quantity.

INTRODUCTION

The upper slopes of the Cascade and Olympic Mountains of the Pacific Northwestern United States support extensive stands of subalpine forests. These forests are dominated by Abies amabilis (Dougl.) Forbes and occupy one of the harsher forest environments of this region. Habitats in this forest zone

generally have strongly seasonal but abundant precipitation, low evaporative demand, persistent snow pack, a short (130 day) growing season, low average soil and air temperatures, and soils that remain unfrozen in winter (Hinckley et al this volume).

Recent studies have indicated that a much greater proportion of annual dry matter production and nutrient utilization occurs below the soil surface in these stands than in lowland conifer stands of the same region (Grier et al, 1981, Vogt et al. 1981, Meier 1981). The same research also indicates that carbon and nutrient allocation to below-ground structures increases with stand age. One of the primary objectives of this research has been to identify factors regulating the above- to below-ground production balance in these ecosystems.

The purpose of this paper is to provide a summary of our current state of knowledge of how soil water status, soil atmosphere, and nutrient availability influence root production in subalpine conifer forests of the Pacific Northwestern United States.

THE ABIES AMABILIS FOREST ZONE

The Abies amabilis forest zone (Franklin and Dyrness 1973) constitutes the largest portion of subalpine forests in Oregon and Washington. This zone is named for the potential climax species in these forests. Abies amabilis (Dougl.) Forbes. This forest zone ranges in elevation from about 500 to 1500 meters and occurs primarily on the western slopes of the Olympic and Cascade Mountains. Figure 1 shows the distribution of Abies amabilis zone forests in Oregon and Washington.

Since these forests lie on the windward slopes of the mountains, they are strongly influenced by maritime weather patterns and tend to have cold, damp climatic conditions. Reported mean annual temperatures range closely around 5.5°C and annual precipitation generally averages about 2500 mm/yr (Franklin and Dyrness 1973). Eighty percent, or more, of the annual precipitation occurs as snow. Consolidated late-winter snow



Figure 1. Approximate occurrence of *Abies amabilis* zone in Oregon and Washington. From Franklin and Dyrness (1973).

pack depth in these forests averages about 3 m; in heavy snow years, spring snow accumulations can exceed 6 m. Because of heavy accumulations and low temperatures, snowpacks usually last into June and occasionally are still present in early July.

The topography occupied by these forests is steep. Soils are rocky, young, and reflect the nature of their parent material. The soils are generally podzolic.

Forests in this vegetation zone are dominated by *Abies amabilis*, at least in later stages of succession. Tree species common in early stages of succession can include *Abies amabilis*, *Abies procera*, *Pseudotsuga menziesii*, *Tsuga heterophylla*, and occasionally *Tsuga mertensiana*. Late-successional forests are dominated by the more shade-tolerant of the above species, primarily *Abies amabilis* and one or both of the *Tsuga* species. Ericaceous species are well represented in understory vegetation with various species of *Vaccinium* being common. Common herbaceous species include *Achlys triphylla*, *Rubus pedatus* and *Tiarella unifoliata* especially in more mesic habitats. Beargrass (*Xerophyllum tenax*) is a common associate.

RESEARCH SITES

Research described in this paper was conducted at one of three sites in the Cascade Range of Oregon and Washington. These sites were the Findley Lake Research Area near Seattle, Washington, the upper Cowlitz Watershed near Mt. St. Helens, Washington, and the Wildcat Mountain Research Natural Area in the central Oregon Cascades.

The Findley Lake Research Area has been the focus of a series of intensive studies of production and nutrient

cycling processes, tree physiology and mycorrhizal ecology. Much of the emphasis at this site has been on belowground processes. Research here has been concentrated on two stands that are presently 30 and 190 years-old. Soils of this research area are formed in volcanic ash overlying andesitic volcanic rock. The site is described in considerable detail by Grier et al. (1981).

The upper Cowlitz Watershed site was originally established to determine the effect of Mt. St. Helens tephra deposition on belowground processes in upper-slope forests. This study was later expanded to include research on the effect of soil gas composition on root growth. Three study stands were established in the upper Cowlitz River watershed at Elk Pass, Lambert Creek and Chambers Lake. All three sites were in mature, *Abies amabilis*-dominated forests located along a gradient of decreasing depth of tephra deposits from the May 1980 eruption of Mt. St. Helens. The Elk Pass site, nearest Mt. St. Helens, received tephra deposits 15-18 cm deep. The Lambert Creek site was intermediate receiving 5-8 cm of tephra. Chambers Lake was about 50 km from the volcano and received about 3 cm of tephra. Stands at the three sites were chosen for their similarities in forest species composition, stand structure and understory. The Elk Pass and Chambers Lake sites are the most similar; Lambert Creek is at about 300 m lower elevation. Soils at these three sites were formed in other deposits of Mt. St. Helens tephra.

The Wildcat Mountain Research Natural Area is located in the Cascades of Oregon near the town of McKenzie Bridge. Two 130-year-old stands were studied here; one was an early successional *Abies procera*/*Pseudotsuga menziesii* stand with an understory tree layer of *Abies amabilis*. The other stand was an *Abies amabilis*/*Tsuga mertensiana* stand again with a well developed understory layer of *Abies amabilis*. Soils are formed in fractured andesite and volcanic ash. The two research stands here are described in detail by Fujimori et al. (1976).

METHODS

Methods used in this study have mostly been described in detail elsewhere (Grier et al. 1981, Vogt et al. 1981, Meier 1981, Grier & Milne 1981, Keyes 1982, Teskey 1982). A brief description is provided here for the sake of continuity.

Tree biomass was calculated from regressions on stem diameter derived from destructive analysis (Grier et al. 1981, Grier and Milne 1981). Shrub and herb biomass, forest floor and fallen logs mass and mass of standing dead trees were determined by area harvest (Grier et al. 1981). Aboveground net primary production was obtained using measurements of stem diameter increment with biomass regressions; these were

combined with litterfall and mortality and understory increment determinations to estimate annual dry matter production (Grier et al. 1981). Belowground biomass and root production was estimated by sequential soil coring and sorting of roots from soil cores (Grier et al. 1981, Vogt et al. 1981). Mycorrhizal production was estimated by hand sorting of mycorrhizal roots from soil cores obtained roughly monthly throughout the year. Nutrient cycling information was obtained by chemical analysis of plant tissues, forest floor, soil, litterfall and other pathways of nutrient movement.

Soil gas composition was determined by weekly sampling of soil atmosphere using a syringe and access tubes. Soil atmosphere O_2 and CO_2 were determined using a gas chromatograph. Effects of soil atmosphere O_2 and CO_2 on root and top growth of *Abies amabilis* was conducted in a controlled environment chamber. Photoperiod was 12 hours. Daylight air temperature was 15°C while night temperature was 6°C. Root systems were sealed into a gas flow system that permitted control of input O_2 and CO_2 concentrations. These ranged from 2% to 20% O_2 and from 300 ppm to 8% CO_2 in factorial combination. Trees were grown under these conditions for 4 months then harvested and fine root and foliage biomass was determined.

RESULT AND DISCUSSION

Belowground characteristics of subalpine forests

Table 1 lists fine root, total and leaf biomass of a number of northwestern subalpine forest ecosystems together with total biomass, and leaf biomass. Similar data from a number of lowland ecosystems are provided for comparison. One obvious feature of the subalpine forests is their consistently large fine root biomass and the rather narrow range of this biomass. In contrast, the lowland forests had, with a single exception, half or less the fine root biomass of subalpine forests. The lowland ecosystem having a large fine root biomass was a low-productivity Douglas-fir stand growing on a coarse, gravelly outwash soil.

Table 2 gives major components of above- and belowground production in some subalpine and lowland ecosystems. In all subalpine ecosystems examined thus far, fine root production amounts to half or more of total ecosystem dry matter production (Grier et al. 1981). Mycorrhizae, another belowground component, account for an additional 10-15% of annual production (Vogt et al. 1982).

This large allocation to belowground structures has several implications. One implication is that these ecosystems are far more productive than aboveground measurements alone would indicate. Another implication is that allocation of large amounts of energy to fine roots and mycorrhizae is a mechanism that helps adapt subalpine species to their rigorous environment.

Several questions arise from these implications: 1) Are observed allocations genotypically or phenotypically determined? That is, does the site "select" for genotypes that make large investments in root systems or are individual trees capable of acclimating to site-imposed stress. 2) What environmental factors result in increased allocation of carbon belowground or cause selection for genotypes which allocate more carbon belowground?

Because of the harsh subalpine environment, a variety of site factors could influence root biomass and production. Although the list of factors is potentially large, the most likely factors to which trees must acclimate appear to be soil atmosphere composition, water availability, and mineral nutrition. In many ways, temperature, through its effect on nutrient mineralization, organic matter decomposition and plant physiological processes is the obvious overriding stress. But, our primary interests were in learning how temperature influences forests by its effect on these factors.

Detritus accumulation in subalpine forests

One major characteristic of subalpine forests in the U.S. Pacific Northwest is the large accumulation of detrital material on the soil surface. In mature stands, forest floor accumulations alone are almost always in excess of 100 Mg ha⁻¹ and frequently exceed 200 Mg ha⁻¹ (Williams and Dyrness 1967, Grier et al. 1981, Vogt et al. in press). Standing dead trees and fallen logs can easily add an additional 200 Mg ha⁻¹ (Grier et al. 1981). These large accumulations result from a combination of low decomposition rates, relatively modest above-ground litterfall inputs and large inputs to forest floor from fine root turnover (Vogt et al. 1983). These large accumulations of organic matter also represent large nutrient accumulations; at an average nitrogen concentration of 0.85% (Meier 1981), 100 to 200 Mg ha⁻¹ of organic matter contains 850 to 1700 kg ha⁻¹ of nitrogen. Most likely because of this, in mature subalpine forests 60 to 80% of fine root biomass is located in the forest floor (Grier et al. 1981).

Site water relations

As noted earlier, the large fine root biomass and production in subalpine and some lowland ecosystems appears to be an adaptation to harsh site conditions. In other words, trees growing on these sites are forced to allocate substantial amounts of carbon to their root systems to survive in this environment.

One site factor possibly responsible for the large fine root biomass could be the site water balance. However, a considerable body of information would argue against this possibility. Gholz

Table 1. Fine root, foliage, and total biomass in some subalpine and adjacent lowland forests of western Oregon and Washington. Biomass values are in Mg ha⁻¹

Site	Elev. (m)	Average Age (yr)	Major ¹ Species	Roots <5mm	Total Biomass	Leaf Biomass	Foliage/ Root	Source
<u>Subalpine Forests</u>								
Findley Lake	1140	23	ABAM	9.2	77.9	13.6	1.48	Grier et al 1981
Findley Lake	1140	185	ABAM	12.8	585.1	21.6	1.69	Grier et al 1981
Elk Pass	1200	260	ABAM TSME	9.8	632.2	19.3	1.97	Grier unpubl. Vogt unpubl.
Chambers Lake	1330	280	ABAM TSME	9.0	472.4	18.5	2.06	Grier unpubl. Vogt unpubl.
Wildcat Mountain	1500	130	ABAM TSME	13.2	574.6	19.7	1.49	Grier unpubl.
Wildcat Mountain	1220	130	ABPR	11.1	1149.2	17.5	1.58	Grier unpubl.
<u>Lowland Forests</u>								
Pack Forest	120	50	PSME	4.5	555.8	16.0	3.56	Keyes & Grier 1981
High productivity								
Pack Forest	120	50	PSME	10.5	306.2	10.0	0.95	Keyes & Grier 1981
Low productivity								
Cascade Head	100	30	TSHE	2.4	373.4	22.3	9.29	Grier unpubl.
Entiat ²	1070	70	PIPO	1.6	146.3	6.1	3.81	Grier unpubl.

¹ ABAM - Abies amabilis
 ABPR - Abies procera
 PIPO - Pinus ponderosa
 PSME - Pseudotsuga menziesii
 TSHE - Tsuga heterophylla
 TSME - Tsuga mertensiana

² Entiat study site is located on the eastern slopes of the Cascade Mountains where timberline is higher. This is a lowland forest for the eastern Cascades.

Table 2. Above- and belowground net primary production in some subalpine and adjacent lowland ecosystem of Oregon and Washington. Productivity values in Mg ha⁻¹ yr⁻¹.

Site	Elev.	Age	Major Species	Total Product.	Belowground Production ²	Belowground Total%	Source
<u>Subalpine forests</u>							
Findley Lake	1140	23	ABAM	18.3	11.8	64.7	Grier et al 1981
Findley Lake	1140	185	ABAM	16.8	12.2	72.9	Grier et al 1981
Elk Pass	1200	260	ABAM TSME	16.2	10.3	63.5	Grier unpubl.
Chamber Lake	1330	280	ABAM TSME	14.6	10.0	68.5	Grier unpubl.
Wildcat Mtn.	1500	130	ABAM TSME	15.8	10.9	68.9	Grier unpubl.
<u>Lowland forests</u>							
Pack Forest	120	50	PSME	17.8 ³	4.1	23.0	Keyes & Grier 1981
High productivity							
Pack Forest	120	50	PSME	15.4 ³	8.1	52.6	Keyes & Grier 1981
low productivity							
Cascade head	100	30	TSHE	35.7	7.0	20.0	Grier unpubl.

¹ ABAM Abies amabilis ABPA Abies procera
 PSME Pseudotsuga menziesii TSHE Tsuga heterophylla
 TSME Tsuga mertensiana

² Calculated from regression on root biomass for Wildcat mountain stands, Elk Pass and Chambers Lake sites. Belowground production includes mycorrhizae for the Findley Lake sites only. Coarse root (>5 mm) production included for all stands.

³ Mortality and branch fall not included. These generally add 5-15% to aboveground productivity.

(1982) and Grier and Running (1977) have shown large leaf areas in these subalpine forest ecosystems and have associated this with low evaporative demand. Similarly, Zobel et al. (1976) made direct measurements of growing season leaf water potential in a number of subalpine stands and aside from mid-day depressions did not find significant water stress.

Teskey (1982) conducted field experiments to determine if the large biomass of fine roots in *Abies amabilis* was required to maintain tissue hydration. In this study, leaf water potential was measured on selected trees hourly through a day. Before dawn of the following day, roughly 35% of the root system of one-third of the trees and 50% of another third were cut at the root collar. The remaining third remained as controls. Leaf water potential was again measured throughout the day. This experiment was performed several times through two summers; results are reported in detail by Teskey (1982) and by Hinkley et al., this volume. Figure 2 is from the report by Teskey and shows the development of leaf water potential during the hottest, driest day that measurements were made. As can be seen from these data, removal of roughly a third of the root system had no discernable effect on leaf water potential or leaf conductance. Even removal of half of the root system had relatively little effect. Capacitance by stemwood was minimal; completely severed trees developed low leaf water potentials rapidly after cutting. Root grafting was not likely since trees used for the study were selected for maximum distance from their neighbors. We interpret the results of this experiment and the work by Zobel et al. (1979) as indicating that *Abies amabilis*, and probably other species adapted to this environment, have considerably more root system than is required to maintain a favorable water status for photosynthesis during the growing season. The possibility remains, however, that the large fine root biomass of subalpine species is an adaptation to avoid winter desiccation. Dry, sunny periods with low relative humidity occur regularly during the winters in this region. Lowland forests occasionally suffer foliage damage by these "East Winds." If large fine root biomass were an adaptation to these conditions, one would expect these levels to be maintained through the winter. In fact, fine root biomass in these stands declines to fairly low levels in mid-winter (Grier et al. 1981).

Soil atmosphere composition

As noted earlier, a high proportion of fine roots in subalpine forests are located in the forest floor. An average value for mature *Abies amabilis* stands is about 60% of total fine root biomass in the forest floor. We have observed stands with over 90% of the root system in organic layers. There are a number of possible explanations for this concentration of roots in a relatively thin (5-10 cm) surface layer. The two most likely explanations are nutrient availability and soil atmosphere composition.

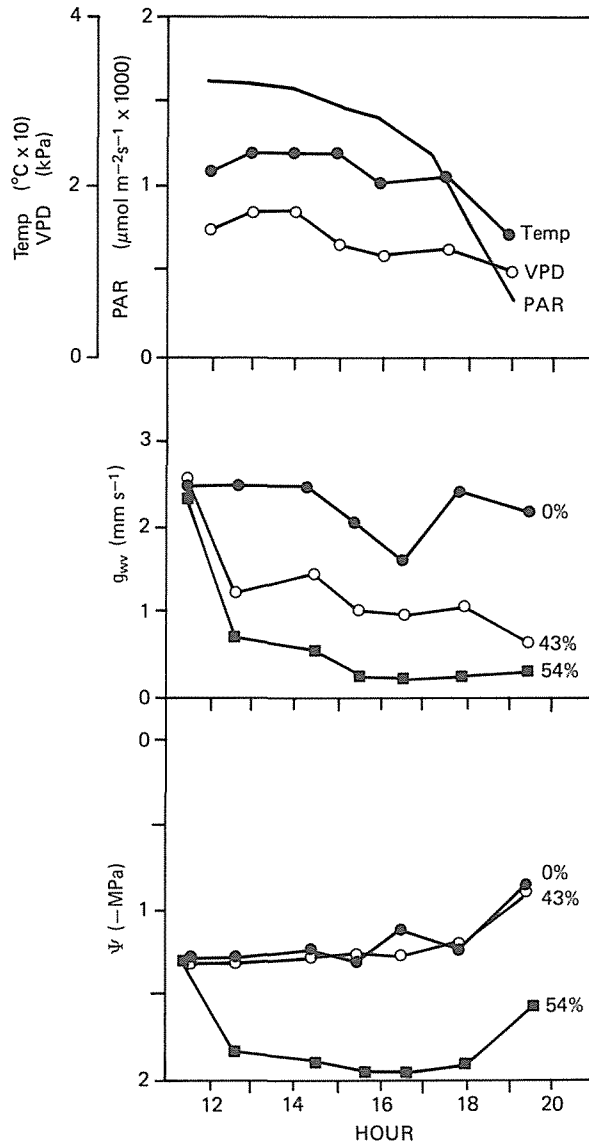


Figure 2. Root severing experiment conducted 31 July 1980. Upper graph shows environmental data: air temperature (Temp), vapor pressure deficit (VPD) and photosynthetically active radiation (PAR). Lower graphs show the effect of root cutting on stomatal conductance (g_{wv}) and xylem water potential (Ψ). The percent of root system which was removed is indicated on each graph (control = 0%).

In an early study of soil respiration on small (2m²) trenched plots, we found no difference in soil CO₂ production between trenched and control plots. These plots had been trenched 3 years before this study, so decomposer response to freshly cut roots should have declined. This lack of response to eliminating root and mycorrhizae respiration led us to suspect an oxygen limitation on soil processes in these subalpine ecosystems. Thus, the possibility existed that decomposers responded to elimination of O₂ use by roots and mycorrhizae by increasing their activity. For this reason, we felt that rates of oxygen diffusion into the soil could

play a role in regulating root distribution in these ecosystems. The large fine root and mycorrhizae biomass in these ecosystems together with the large decomposer biomass in forest floors could potentially have a large demand for oxygen. Competition between root systems and decomposers for oxygen could cause concentration of roots near the soil-atmosphere interface.

To examine this possibility, we installed soil gas sampling probes in a number of *Abies amabilis* zone ecosystems. Several of these had received tephra deposits from the May 1980 eruption of Mt. St. Helens. The Findley Lake site served as a control. Gas sampling probes were placed 3 cm above, and 3 and 20 cm below the forest floor surface at 5 locations in each stand. Soil gas samples were taken weekly between May and November and analyzed for O_2 and CO_2 concentrations using a gas chromatograph.

Table 3 gives the seasonal average soil O_2 and CO_2 concentrations for the control site and the site with the deepest tephra accumulation. Values for the other two tephra-covered sites were intermediate. Clearly, oxygen concentrations in the soil profile are only slightly different from that of the atmosphere even for the tephra covered site. Moreover, while soil atmosphere CO_2 concentrations were consistently greater than the 330 ppm level we obtained for the atmosphere, concentrations are well within ranges reported for agricultural soils (Gunn and Trudgill 1982).

Table 3. Average growing season soil oxygen and carbon dioxide concentrations for tephra covered (Elk Pass) and control (Findley Lake) research sites.

Oxygen (%)						
Elk Pass			Findley Lake			
depth (cm)	\bar{X}	S	N	\bar{X}	S	N
+ 3	20.3	0.88	14	21.0	0.88	13
- 3	20.0	1.00	16	20.4	0.61	17
-20	19.2	1.21	13	20.4	0.87	16

Carbon Dioxide (%)						
	\bar{X}	S	N	\bar{X}	S	N
+ 3	0.25	0.08	14	0.16	0.15	20
- 3	0.54	0.40	16	0.42	0.25	24
-20	1.34	0.62	13	0.74	0.34	23

¹Depth values represent distances above (+) or below (-) the forest floor surface.

In spite of near-atmospheric concentrations of O_2 and CO_2 in the soil atmosphere during our period of observation, *Abies amabilis* appears to be tolerant of wide fluctuations in soil atmosphere composition. We conducted a factorial experiment growing 3-4 year-old *Abies amabilis* in pots with inlet gas flow having regulated O_2 and CO_2 concentrations from 2% to 20% O_2 and from 300 ppm to 8% CO_2 in factorial combination. Ambient air served as a control. There were no significant seedling growth responses to treatment over the 4 month experiment, either above or below the soil surface.

To summarize our experience, soil atmosphere composition in broadly representative *Abies amabilis* ecosystems is near that of the atmosphere, at least while the soil is snow free. Moreover, *Abies amabilis* appears tolerant of low

oxygen and high carbon dioxide levels in the rooting zone during the growing season. Soil atmosphere does not appear to influence root growth or distribution.

Mineral nutrition and root production

Because of slow decomposition, nutrient mineralization and nutrient availability are low in *Abies amabilis* zone ecosystems. Nitrogen levels in forest floor and soil of these forests is low relative to lowland ecosystems of the region (Table 4) and ammonium is the dominant ionic nitrogen form. Nitrate is generally present at or below detection limits in these ecosystems. Nitrogen mineralization rates are also low in *Abies amabilis* ecosystems. Table 5 shows mineral nitrogen concentrations in extracts from incubated soils. Those from Findley Lake are from a subalpine site; here they are compared with results from lowland sites of the region.

Table 4. Extractable NH_4^+ and NO_3^- in forest floor of some subalpine and lowland soils of Oregon and Washington.

Site	Major Species	Age	ppm			
			NH_4^+	N	NO_3^-	N
Subalpine			X	S	X	S
Findley	ABAM	23	52	16	T	-
	ABAM	185	38	15	T	-
Wildcat Mountain	ABAM	130	32	14	T	-
	ABPR	130	75	34	T	-
Lowland Cascade Head	TSHE	129	95	28	5.3	3
Pack Forest	PSME	45	67	29	1.2	0.7

¹Soils were sampled in June. Extractions were made in 2N KCl for 24 hours; extraction started within 5 minutes of the time sample was removed from profile.

Table 5. Nitrogen mineralization potential¹ in some subalpine and lowland soils of western Oregon and Washington.

Site	Major Species	Age (yr)	NH_4^+ + NO_3^- Nitrogen (ppm)			
			Forest Floor	Floor	Mineral Soil 0-15 cm	S
			X	S	X	S
Subalpine						
Findley Lake	ABAM	23	145	43	28	11
	ABAM	185	45	19	5	3
Wildcat Mountain	ABAM	130	120	33	4	2
	ABPM	130	155	42	30	12
Lowland						
Cascade Head	TSHE	30	295	65	45	17
	TSHE	129	320	92	60	15
Pack Forest	PSME	50	150	53	39	19
Low site	PSME	50	275	95	60	20
High site						

¹Eight week incubation at 20°C and field moisture capacity. Nitrogen extracted in 2N KCl as determined using Technicon Autoanalyzer. Sampling done in late October.

In Figure 3 belowground production expressed as a percentage of total net primary production, is plotted against the same index of nitrogen availability described in Table 5 for a number of ecosystems in western Oregon and Washington. There is a clear inverse relationship between nitrogen availability (and presumably availability of any limiting nutrient) and carbon allocation to roots and mycorrhizae.

Based on this observation, it seems reasonable to speculate that the large investment in root biomass and mycorrhizae and their rapid turnover is a response both to low nutrient (nitrogen) availability in soil and the form of nitrogen

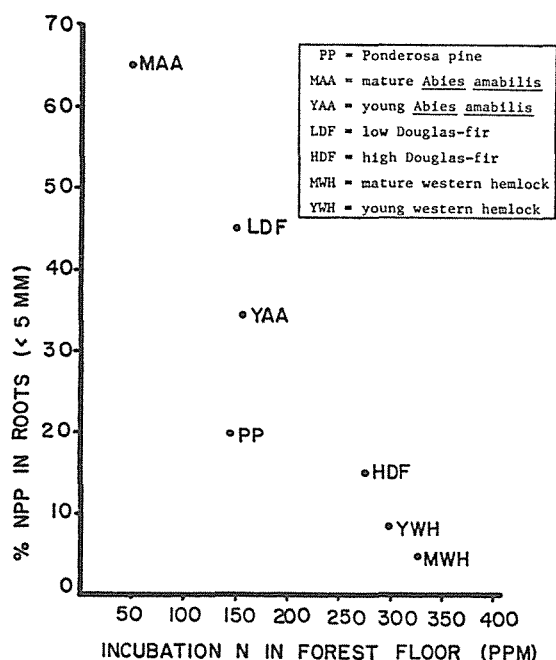


Figure 3. Relation between forest floor nitrogen availability (NH_4^+ NO_3^-) and the proportion of total net primary production occurring as fine roots. Incubation N was obtained by extracting NH_4^+ and NO_3^- with 2N KCl after a 6-week incubation at 20°C and field moisture capacity.

available. Ammonium, being a cation, is generally retained against mass flow and diffusion by the soil cation exchange complex. This means that a root (or mycorrhizal hyphae) would have to be close to a retained ammonium ion for uptake to occur. The same requirements would exist for anion nutrients such as sulfate and phosphate. These ions are strongly sorbed by the soil (Johnson 1975). Intensive exploration of the soil by large fine root and mycorrhizae biomass and re-exploration by root production and turnover appears to be an effective, if energy-intensive adaptation to a site where nutrients are tightly retained and sparingly available.

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